Observations of the biology and immature stages of the sandgroper *Cylindraustralia kochii* (Saussure), with notes on some congeners (Orthoptera: Cylindrachetidae)

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Abstract – Field and laboratory observations of *Cylindraustralia kochii* are presented with notes on some congeners. Nymphs and adults create galleries in moist soil by compression of the soil with their powerful fore legs, burrowing to depths of up to 1.9 m. During the cooler months and 1–2 days after rain, sandgropers commonly burrow long distances close to the soil surface producing conspicuous raised trails. Adults and nymphs of various sizes were found throughout the year. Eggs and early immatures of the genus (and family) are described for the first time. Pedicellate eggs of *C. kochii* were suspended singly in closed chambers 40–190 cm deep in moist soil. A 'larval' stage hatches from the egg and moults to a first instar nymph while still in the egg chamber. Five nymphal instars are indicated by morphometric and morphological data. Eggs are laid from autumn to spring but hatching was only observed in mid summer. A duration of at least 12 months is indicated for first instar nymphs, so the complete life cycle may extend over several years. Examination of gut contents revealed that sandgropers are omnivorous, consuming a wide array of plant, fungal and arthropod material. Plant food included root, stem, leaf, flower and seed tissue. Cannibalism occurred in one very dense population of *C. kochii*. Otherwise, no insect predators or parasitoids were encountered. Associated organisms included gregarines and *Amoeba* (Protista) in the intestines, rhabditid nematodes in the genital chambers of adults, and six species of mesostigmatid and astigmatid mites which adhered externally to the body. Nymphs and adults produce an odorous, probably defensive secretion from a pair of abdominal glands.

**Key words:** subterranean insects, ethology, ecology, parasites

INTRODUCTION

Sandgropers, once regarded as degenerate mole crickets (e.g., Tindale 1928), are now classified with the short-horned grasshoppers (suborder Caelifera) and form the family Cylindrachetidae within the superfamily Tridactyloidea (Rentz 1996). Included with them in this superfamily are the Tridactylidae ('pygmy mole crickets') and Ripipterygidae ('mud crickets') (Günther 1994; Flook *et al.* 1999). All cylindrachetids are burrowing insects, highly modified for a subterranean existence. The body shape is cylindrical, the fore legs are highly modified for digging, the reduced mid and hind legs recess into the sides of the abdomen, simple eyes replace the compound eyes, antennae and cerci are reduced, and wings are entirely absent (Figures 1–3). Of all the orthopteroid insects, they are considered to be the most strongly modified morphologically for a subterranean life (Kevan 1989).

In the most recent revision of the family (Günther 1992), three genera and 16 species were recognized.

Fourteen species are Australian, one is Argentinean and one putatively occurs in New Guinea. Günther erected a new genus, *Cylindraustralia*, to contain 13 of the Australian species. Prior to his revision, all known Australian species were placed in *Cylindracheta* Kirby, a genus Günther restricted to one species from the 'Top End' of the Northern Territory. *Cylindraustralia* species occur widely across the Australian continent but are absent from the south-eastern portion.

Although the taxonomy of cylindrachetids has been reasonably well studied, their biology has received scant attention (Barrett 1928; Tindale 1928; Richards 1980; Günther 1992; Rentz 1996). Some published information is misleading or incorrect and nothing has been recorded hitherto of the eggs and early immature stages. Of course, living almost wholly subterranean lives, the insects are rarely observed and make difficult subjects for study.

In Western Australia, sandgropers have gained a reputation as agricultural pests, being reported to damage wheat, barley, oats, sweet lupins and
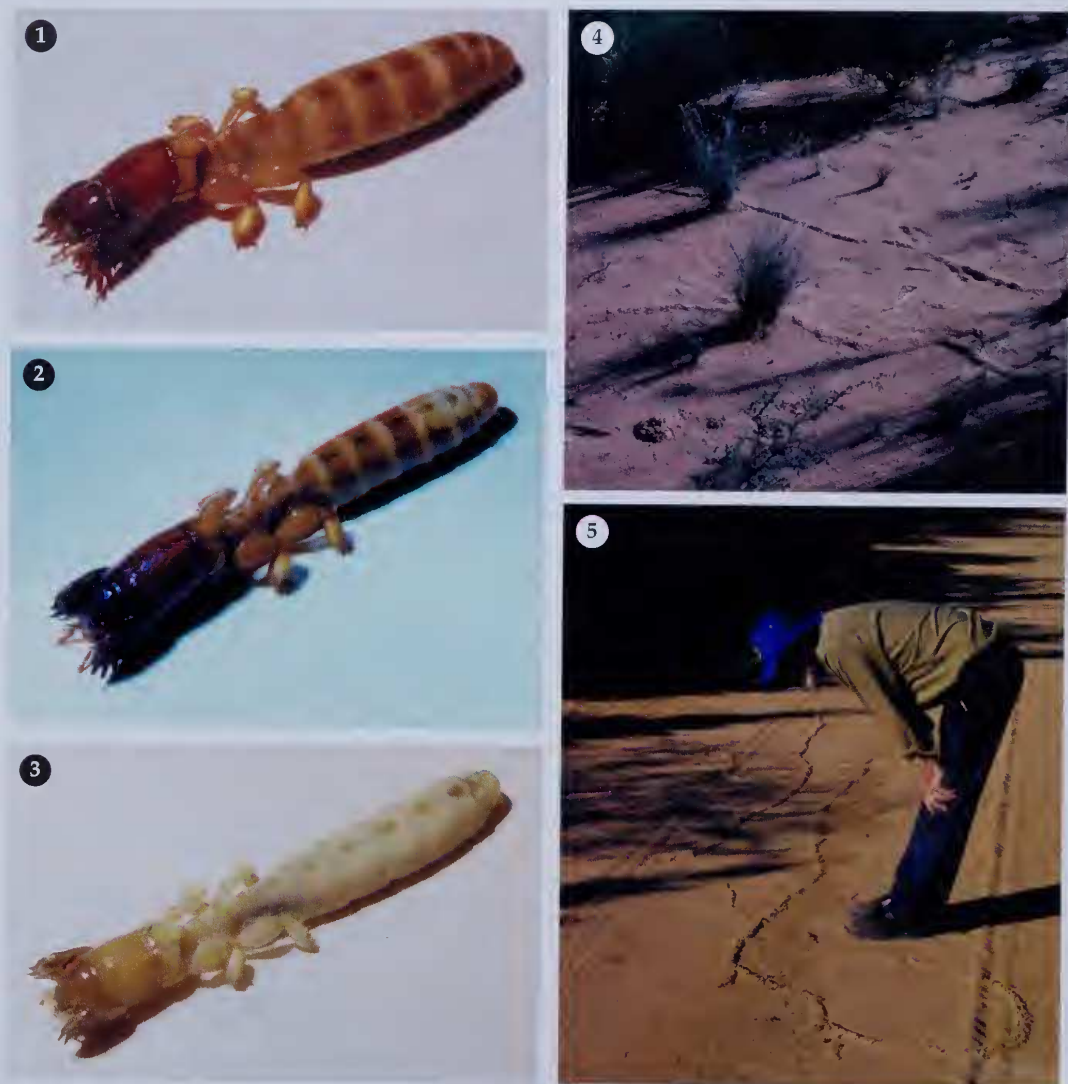
Figures 1–5 *Cylindraustralia kochii.* (1–2) Adult female and male, respectively (note bands of pigmentation around abdomen, in male interrupted dorsally on segments 7–9). (3) Last stage nymph (note absence of abdominal pigmentation; dark 'marks' along dorsal median line are gaps in underlying fat body visible through transparent integument). (4–5) Surface trails produced by adults burrowing just beneath surface of ground: (4) simple trails in natural bushland; (5) branched trails on compacted sand surface of farm road.

tagasaste between Perth and Geraldton (Richards 1980; Rentz 1996; Wiley 2000). Only anecdotal and circumstantial evidence, though, was produced by these authors to show that sandgropers were the cause of the observed plant damage.

While the insects themselves are rarely encountered, their characteristic trails (Figure 4) are a common sight on bare sandy ground in Western Australia. Two species (*C. kochii* (Saussure) (syn. *psammophila* (Tindale)) and *C. tindalei* Günther) are known to be extant in and around Perth.

The present study was undertaken in an attempt to elucidate the life histories, behaviour and ecology of sandgropers.

MATERIALS AND METHODS

Over 900 spirit-preserved specimens of *Cylindraustralia* in the collection of the Western Australian Museum were examined in this study. Most were collected by the author from 2002–2005, the remainder being donated by members of the

farming community and the general public in response to a media appeal. By far the bulk of the material studied was comprised of *C. kochii* while most of the remainder consisted of *C. tindalei*.

Although sandgropers have occasionally been found in pitfall traps, the author's deployment of gutter traps and pitfall traps combined with drift fences at a number of sites failed to yield specimens. Following on foot close behind farm ploughs turning over soil under pasture yielded many specimens. Others were obtained from near-surface galleries: by driving back and forth along sandy roads and firebreaks on the margins of bushland shortly after rain, it was possible to recognize fresh trails where they crossed the vehicle's tyre tracks (Figure 5). Most specimens obtained for this study, however, were turned up by digging with a spade beneath pastures and weeds on farms.

Study sites where significant work was undertaken are as follows (short-hand names used in this paper appear in quotation marks): "Dandaragan site"– Annamullah Farm, 6 km NNE of Dandaragan, 30°38'S, 115°45'E; "Horrocks site" – Willi Gulli North Farm, 18 km W of Northampton (2 km E of Horrocks), 28°22'S, 114°27'E; "Eurardy site" – Eurardy Station, 89 km N of Northampton, 27°34'S, 114°40'E; M. and D. Webb's farm, 23 km E of Northampton, 28°18'52"S, 114°51'58"E; and "Great Sandy Desert", various sites approximately 220–280 km SE of Broome, between 19°04'13"S, 123°44'05"E, and 19°17'52"S, 124°26'27"E.

Various methods of killing and preserving specimens were trialled. For the purposes of later dissection, best results were obtained by freezing specimens. Where this was impractical, freshly killed specimens were injected with and stored in 10% formalin (although injection caused the abdomen to inflate and extend). Several specimens were killed by spraying the head and thorax with electrician's freezer and were then immediately dissected in saline to check for living parasites or commensals in the gut, abdominal cavity and genital tracts.

Live specimens were maintained in containers of moist sand or sandy loam with various plants: Cape Weed (*Arctotheca calendula*), Wild Oats (*Avena fatua*), and seedlings germinated from commercial 'mixed budgie seed'. Glass-bottomed and clear plastic containers permitted observations of burrowing activity. Eggs were reared on tissue wads in glass vials in humid boxes. The boxes were kept at room temperature (18–30°C) and open vials of saturated salt solution provided moderate humidity.

Specimens were identified by comparison with specimens in the Western Australian Museum determined by Dr Kurt Günther and by means of Dr Günther's 1992 revision of the family Cylindrachetidae. Some specimens from the

Horrocks and Great Sandy Desert sites could not be matched to any of Günther's taxa and appear to represent undescribed species referred to below as 'Species A' and 'Species B', respectively.

The pronotal width of all specimens was measured to determine the number of instars. The pronotum is a rigid structure that is easily and reliably measured across its greatest width.

Population sampling at the Dandaragan site was undertaken approximately every second month although the October sample was not in sequence with the rest. The method used was to excavate a large pit at least 1 x 2 m in area and 1–2 m deep using a spade and trowel and to collect every specimen encountered as the soil was turned over. Excavation required 2–4 days.

OBSERVATIONS AND DISCUSSION

Life Stages and Morphology

Adults

Apart from having completely developed genitalia, adults are distinguishable from nymphs in having the abdominal integument wholly or largely tan-coloured (Figures 1, 2) (in males of *C. kochii* the tan pigmentation is usually broken by narrow, colourless, intersegmental bands). The abdominal integument of all nymphal stages, by contrast, is completely colourless and, being transparent, the abdomen appears white or cream because of the underlying fat body (Figures 3, 11).

Males and females are similar in size. Among a sample of *C. kochii* adults from the Dandaragan site, pronotal widths of males ranged from 6.75–8.20 mm (mean 7.35 ± 0.33, n = 20) and of females from 6.80–8.30 mm (mean 7.4 ± 0.44, n = 14). The sexes are also very similar morphologically but can be distinguished by the external genitalia. As Günther (1992) noted, males possess a pair of short, stout spines on the paraprocts near the insertions of the cerci (Figure 13). Females lack these spines and, instead, possess a pair of rudimentary gonovalves, the tips of which sometimes protrude slightly beyond the apical margin of the 8th abdominal sternite (S8, Figure 12). In *C. kochii* (but not other species), adult males are further distinguished by a large unpigmented patch on the dorsal side of abdominal segments 7–9 (Figure 2).

Eggs

Eggs were first observed in the oviducts of dissected females of *C. kochii*. These oviducal eggs were elongate-ovoidal, *c.* 7.0 mm long and 3.3 mm in diameter, flat to slightly concave on one side (thus being bilaterally symmetrical), and had a tiny appendage *c.* 0.5 mm long anteriorly (Figure 6). The chorion was smooth, unsculptured and translucent
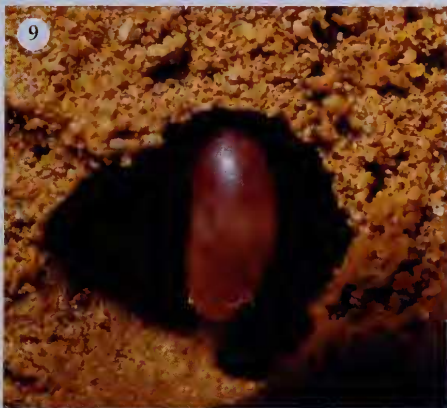
Figures 6–11   *Cylindraustralia kochii*: (6) mature eggs dissected from oviduct (for detail of apical appendages, see Figures 21–23); (7) laid eggs showing attachment pedicels and adhesive disks with adherent sand grains (collected in October, chorions dull and opaque); (8) vertical section of earth showing two freshly laid eggs suspended in their chambers (upper egg has a drop of ground water on right side and a fungus grows on chamber floor); (9) freshly laid egg with red chorion; (10) larva shortly after eclosion (for more details see Figures 24–26); (11) newly emerged first instar nymph with its eggshell.

off-white. The appendage consisted of a doughnut-shaped mass of gelatinous material about 0.7 mm in diameter attached to a central disc which was in turn connected axially to the egg by a short flexible stalk or pedicel (Figures 21–23). At 400x magnification the gelatinous mass was observed to consist of tightly packed bundles of fibrils with their free ends outermost. This appendage later proved to be a device for attachment of the egg to the substrate.

Laid eggs of *C. kochii* were first observed *in situ* at the Dandaragan site in May 2003 when over 40 were uncovered, each enclosed in a small chamber (Figure 8). The eggs were suspended from the ceilings of their chambers on short flexible pedicels, the upper ends of which expanded into rounded discs (Figures 7, 24). The discs were firmly cemented to the soil by some substance that proved to be water-insoluble. Otherwise, the eggs were free of contact with the soil. Most eggs in this lot were translucent white (like oviducal eggs) and presumably freshly laid. A few were wholly dark red (Figure 9) while others were white variously mottled with pink. The red/pink pigmentation was confined to the chorion and, in the wholly red individuals, to the stalk and disc as well but never extended to the yolk which was completely colourless. Many eggs, too, bore a drop of clear liquid on one side (Figure 8) – evidently ground water that had trickled down from the chamber ceilings. At the same site in October 2004, 32 eggs were excavated. The majority were wholly or partly pink and only six were pure white but, in all cases, the chorion was dull and opaque.

No laid or oviducal eggs were found for *C. tindalei* but one near-mature egg (4.3 mm long) in an ovariole had a gelationous appendage much like that of oviducal eggs of *C. kochii*. Oviducal eggs of Species B, however, lacked a pedicel and attachment disc. Instead, each egg had a flat apical cap of gelatinous material (*ca.* 0.8 mm diameter) directly and broadly attached to the chorion.

The glueing of eggs to the substrate, and particularly their suspension on pedicels, is something not reported for other tridactyloid families. Eggs of Tridactylidae and Ripipterygidae, lack any sort of appendage as far as currently known. Eggs of one tridactylid have been reported to be laid in batches of 10–20 in the ends of galleries (Urquhart 1973, cited by Günther 1994) while those of ripipterygids are laid singly in excavations made with the gonovalves much as in the manner of acridids (Schremmer 1972; Gambardella 1971; both cited by Günther 1994).

Larva

In the laboratory, eggs eclosed to a pre-nymphal stage or 'larva' (Figures 10, 25–27), the equivalent of the 'vermiform larva' of the Acrididae (Uvarov 1966). The larva was a setose individual of distinctive form enveloped in a thin, transparent membrane (the 'provisional cuticle' of Uvarov). This membrane, unlike that of acridids, lacked setae and spicules but on the median line of the frons had a thin, brownish, sclerotized and slightly serrated carina (Figures 26, 27), presumably an egg-burster. Other characteristics were: fore legs reflexed backwards against body; prothorax much wider than long and slightly biconvex (weakly depressed medianly); and mesothorax not encapsulating hind part of prothorax. This stage is short-lived, the provisional cuticle being shed almost immediately after eclosion from the egg, or at least within a couple of hours, giving rise to the first nymphal instar.

Nymphs

An individual of typical sandgroper form with the fore legs directed anteriorly emerged from the larval skin (Figure 11). In keeping with convention (David Ragge, pers. comm.), this stage should be regarded as the first nymphal instar. It is at first wholly white with pink eyes but gradually (over a period of days) develops tan colouration in the head and thorax as the cuticle hardens and the eyes turn black. These changes occur before the nymph leaves the egg chamber.

Nymphs are much like adults and are comparatively uniform morphologically. However, the development of the external genitalia provides some characters enabling determination of the sex of an individual and (in females) the particular instar to which it belongs. Tentative determination of the number of nymphal instars in *C. kochii* was made possible by measurement of a large number of nymphs of various sizes and the hatching of early stages from eggs in the laboratory.

The size-frequency distribution for all *C. kochii* collected from the Dandaragan site (Figure 28) reveals four peaks suggesting the existence of four nymphal instars. However, as the larger size classes were poorly represented, the histogram may not present an accurate picture. If the relative increase in pronotal width from instar to instar was constant in keeping with Dyar's 'law' (CSIRO 1991), one would expect another peak to occur around the 5.0 mm mark.

Anatomical evidence for the existence of five nymphal instars was found on the eighth abdominal sternite (S8) of females: the vaginal opening is evident from the first instar, and increases in size and shifts rearward with each moult; in later instars, the gonovalves form from the hind margin of S8 (Figures 14–18).

Male nymphs can be recognized by the absence of the vaginal groove and/or developing gonovalves. Additionally, from about the 3rd instar, they possess developing paraproct spines. These are at first
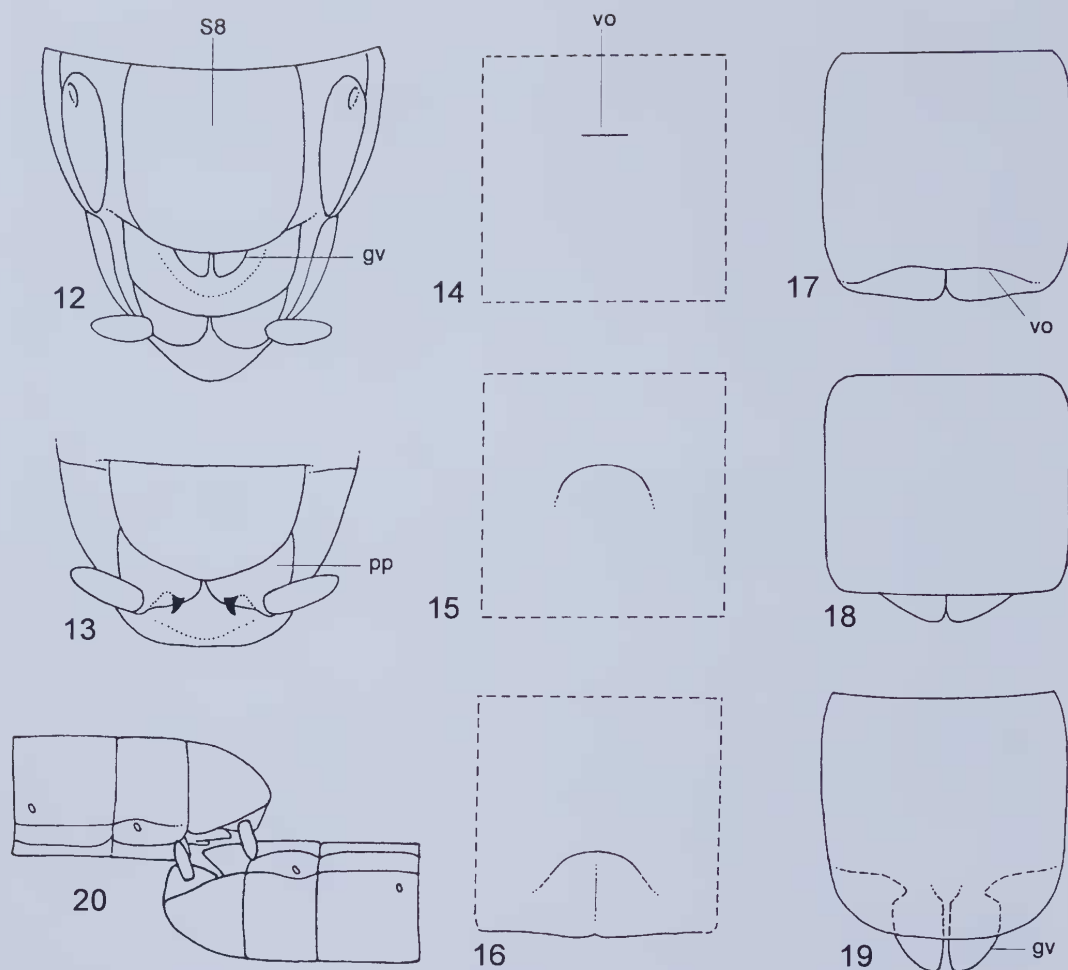
Figures 12–20   Sketches of genital areas of *Cylindraustralia kochii* (not to same scale): (12) underside of apex of
abdomen of adult female, somewhat inflated to show various sclerites and apices of gonovalves
(normally hidden behind 8th sternite); (13) same of adult male, showing copulatory spines (solid black)
on paraprocts (pp); (14–18) eighth sternite of 1st–5th female nymphal instars, respectively, showing
development of vaginal opening and gonovalves (abdominal sclerites of early instars are unsclerotized
and ill-defined, thus approximate boundaries of S8 are indicated by broken lines); (19) eighth sternite of
adult female showing outline of gonovalves; (20) presumed juxtaposition of hind ends of male and
female during copulation (only with this arrangement could copulatory spines of male engage hind
edge of S8 of female, pulling it down and permitting intromission of genital armature into vagina).
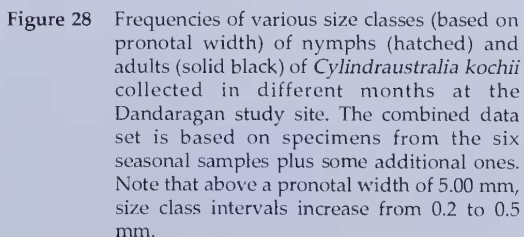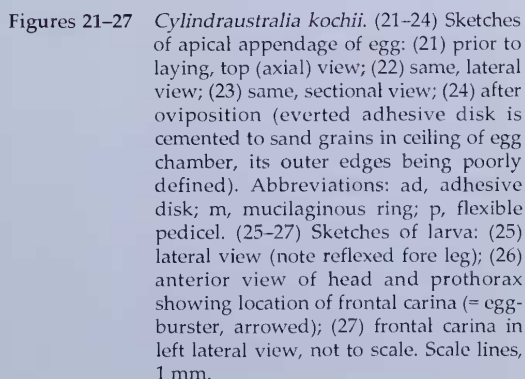Abbreviations: gv, gonovalves; pp, paraprocts; S8, eighth sternite; vo, vaginal opening.

almost imperceptible, colourless tubercles but, in
later instars, they become more pronounced and
more acute and, in the final nymphal instar, acquire
pigmentation and are strongly sclerotized (*cf.*
Figure 13).

Putative stridulatory organ

   A putative stridulatory apparatus on the mouth-
parts of cylindrachetids was described and figured
by Günther (1992) and Rentz (1996). It consists of a
field of microscopic tubercles arranged in rows on

the ventral surface of each mandible and a single
row of about seven short ridges on the opposing
dorsal surface of the basal segment of each
maxillary palpus. Günther noted this apparatus in
both sexes. It is now clear that it occurs in all
nymphal instars as well. Thus, it is unlikely that the
apparatus plays a part in mate-attraction, if in fact it
produces sound at all. I detected no stridulatory
sounds from sandgropers, even when holding them
close to my ear.

   Lawrence and Britton (1994, pl. 2) described and

Figures 21–27   *Cylindraustralia kochii.* (21–24) Sketches of apical appendage of egg: (21) prior to laying, top (axial) view; (22) same, lateral view; (23) same, sectional view; (24) after oviposition (everted adhesive disk is cemented to sand grains in ceiling of egg chamber, its outer edges being poorly defined). Abbreviations: ad, adhesive disk; m, mucilaginous ring; p, flexible pedicel. (25–27) Sketches of larva: (25) lateral view (note reflexed fore leg); (26) anterior view of head and prothorax showing location of frontal carina (= egg-burster, arrowed); (27) frontal carina in left lateral view, not to scale. Scale lines, 1 mm.

Figure 28   Frequencies of various size classes (based on pronotal width) of nymphs (hatched) and adults (solid black) of *Cylindraustralia kochii* collected in different months at the Dandaragan study site. The combined data set is based on specimens from the six seasonal samples plus some additional ones. Note that above a pronotal width of 5.00 mm, size class intervals increase from 0.2 to 0.5 mm.

figured similar patches of minute tubercles (termed 'asperities') on the dorsal surfaces of the mandibles of certain pyrochroid and cucujid beetle larvae but did not attribute any function to them.

Odour glands

Live specimens of *C. kochii* (and other species) often emitted a strong, slightly pungent odour when handled. Günther (1992) noted a number of integumental glands and gland openings in cylindrachetids although he did not discuss their functions. They included a gland opening on the inside of each fore femur, glandular tissue in each mid and hind tibia, a gland opening in each laterosternite of the 3rd abdominal segment and, in males of *C. kochii*, an area of glandular tissue beneath abdominal tergites 7–9. In order to determine the origin of the odour, each of the gland areas of a freshly killed adult of *C. kochii* was excised in turn, crushed between the fingers and the residue sniffed to check for odour. Only the 3rd abdominal segment produced a very strong and lasting odour identical to that noticed in handling live specimens.

Dissection revealed a gland sac attached to each of the two gland openings on the 3rd abdominal segment. These sacs are evidently reservoirs for the gland secretion. An apodeme adjacent to each gland opening provides attachment for a muscle (possibly serving to open or close a valve). The gland openings and sacs were found in adults of both sexes and all nymphal instars. Consequently, the gland secretion is unlikely to play a role in mate attraction and a defensive function seems more likely.

Ecology and Behaviour

Habitat

Field observations, reinforced by museum collection data, reveal that sandgropers inhabit a wide variety of sandy soils including calcareous and siliceous sands and sandy loams. *C. kochii* inhabits diverse habitat types including coastal dunes, sand plains with heath ('kwongan') or shrubland vegetation, red desert dunes with tussock grasses (principally *Triodia* spp.), red sandy loams with open eucalypt woodland and comparatively hard sandy loams with *Acacia* shrubland in the Gascoyne of WA.

Hundreds of specimens of *C. kochii* were collected from agricultural land beneath pastures of mixed weeds including Cape Weed, lupins, clover and exotic grasses or beneath young cereal crops (wheat and barley). Some of this land had been cleared for several decades and the nearest remnants of native vegetation were tens of kilometres away. A smaller number of specimens of *C. kochii* and *C. tindalei* were collected from suburban gardens beneath exotic plants or patches of weeds. Clearly these sandgropers are not dependent on native flora.

Burrowing

Observation of specimens in moist sand in glass-bottomed and clear-sided containers revealed that they create galleries by parting the soil ahead of them with synchronous lateral motions of their fore legs, compressing it to the sides. They do not loosen soil and shift it behind them the way many other burrowing insects do. After each stroke of the fore legs, the insects shuffle forwards on the mid and hind legs. Upward motions of the head, observed in hand-held specimens, may also help compact the walls of the galleries. By twisting the fore body as they progress, the insects are able to compact the soil up and down as well as sideways. The galleries so-formed are smooth-walled, cylindrical and only marginally wider than the insects creating them. Sandgropers move easily and quickly both forwards and backwards within their galleries. Only the mid and hind legs are involved in walking, the fore legs being held stiffly forwards off the substrate.

At the Dandaragan site, adults and large nymphs of *C. kochii* were frequently excavated from depths of 1.0–1.8 m (and given the presence of eggs at 1.9 m, adult females must at times have burrowed to this depth). They could not have gone much deeper because of a gravel layer at 2 m. Smaller nymphs were also found in numbers at depths of 1.5 m or more, although many (if not all) of them would have hatched there. The soil at depths of 40 cm and deeper was very compact and could be cut in blocks. It is testimony to the strength of sandgropers' fore legs that they are able to force a passage through such a compact medium.

Specimens were usually found in horizontal to somewhat inclined burrows, rarely in vertical galleries. In some cases they had found their way into large earthworm shafts which abounded at the Dandaragan site. The galleries of several nymphs and adults that were traced carefully wound erratically downwards, having horizontal, inclined and vertical sections. Several adults and late stage nymphs were encountered at the ends of galleries facing away from the blind ends. How these individuals could have executed turns, allowing them to reverse into these galleries, remains unexplained.

During summer excavations at the Dandaragan site, no live sandgropers were found in the top 20 cm of the soil (the A horizon) which was dry and hard. All specimens occurred in the moist subsoil. The A horizon, however, was almost honeycombed in places with large galleries created on previous occasions. In winter, too, no sandgropers were found in surface soil that had become dry. They ventured into the surface zone only when it was damp following recent rain.

A common habit of sandgropers is to burrow long distances just beneath the surface of the soil producing raised ridges or 'trails' on the surface (Figures 4, 5). Adults of *C. kochii* burrow 1–2 cm beneath the surface, smaller nymphs at comparatively shallower depths. Beneath each raised trail (and scores were examined) was a gallery. The longest continuous section of trail observed was 10 m but the insects may travel much further than this. Trails can persist for weeks or even months and often criss-cross the ground.

In southern Western Australia which has a Mediterranean climate, several sandgroper species produce trails only during the cooler, wet months of the year from about April or May to September or October and only for 1–2 days after soaking rain while the surface soil is moist. Fresh trails appeared throughout the day but not at night. Heavy showers also elicited trail-forming by Species B at the Great Sandy Desert sites in July 2005. Typically, this tropical area has dry winters, receiving its rainfall during the summer monsoon season.

It was sometimes found that sandgropers had backed up one or more metres from the blind (leading) ends of their near-surface galleries. Also, many trails and their underlying galleries branched, especially those occurring on compacted surfaces such as dirt roads (Figure 5). Evidently, when the insects encounter an obstacle, such as soil that is too hard to penetrate, they back up and strike off in a different direction.

Counts of the stages and sexes of sandgropers collected while trail-forming are shown in Table 1. For *C. kochii*, the behaviour seems to involve mainly adult males (92% of specimens), suggesting it could be associated with mate-seeking. A similar but less pronounced trend is noted for *C. tindalei* (72% of specimens). By contrast, both sexes were almost equally represented for Species B. Larger samples will be required to determine if there are persistent species differences here. Given that nymphs as well as adults engage in trail-forming, this behaviour may represent a general dispersal

mechanism. By burrowing close to the soil surface which yields, sandgropers would be able to progress faster and with less effort compared with burrowing at greater depth and still maintain cover.

Soil moisture is clearly important to the burrowing activities of sandgropers. First, it softens the soil (sandy loams often become mortar hard when dry). Second, it binds sand grains ensuring that galleries remain open behind the insects, providing them with a ready means of retreat.

Egg chambers

Egg chambers (Figure 8) measured *c.* 20 mm in length, were smooth and evenly concave at one end and rough at the other. They appeared to have been formed from the blind ends of horizontal or slightly inclined galleries through back-filling of the access burrows following oviposition.

While egg chambers were clearly separate, they were often loosely aggregated. For example, at the Dandaragan site, one group of 19 chambers occurred within a block of soil measuring *c.* 30 x 20 x 20 cm. Within this group there were tighter clusters of 2–5 chambers, the chambers being separated by as little as 1–2 cm. Egg chambers were found at depths of from 40–190 cm.

The process of egg chamber formation and oviposition was not observed but must involve the female in some special manoeuvres including at least two reversals of direction. As a female creates a blind horizontal gallery, the end of which will become the egg chamber, she would face into the blind end. To oviposit in this blind end, she would need to reverse direction and, to attach her egg to the ceiling, must lie on her back. As the egg is extruded from the vagina, the adhesive disc on its anterior (leading) end would contact the ceiling and cement the egg in place. The female must then withdraw and reverse direction again in order to attend to closure of the brood chamber (females having no strongly sclerotized structures at their hind ends that could serve to scrape or push soil). It would be impossible for a female to reverse direction in the narrow confines of a typical gallery, yet I observed nothing that could have served as a 'turning chamber'. However, I did encounter some widened sections of gallery (about twice as wide as usual) which could have been the source of soil used for back-filling access burrows.

Population density and distribution

Other than finding specimens in near-surface galleries following rain, attempts to find sandgropers in bushland areas by means of digging were unsuccessful, even though many holes were dug in areas where trails were common. This would suggest that either the insects were sparsely distributed or they were deeper than my excavations (usually not deeper than 50 cm).

Table 1   Numbers of specimens of sandgropers collected while trail-forming (i.e., burrowing just beneath the surface of the soil causing a raised ridge). The species *C. arenivaga* (Tindale) was observed by the author in the Gibson Desert in 1982.

Species	adult males	adult females	nymphs
C. arenivaga	2		
C. kochii	22	1	1
C. tindalei	13	4	1
C. tindalei?			1
C. tindalei x kochii (?)	1		
Species B	8	7	4

At the Dandaragan site, however, a very different situation prevailed. In mid May 2003 when initial observations were made by the author, a 1 x 1 m hole dug almost anywhere in a paddock carrying only pasture produced one or more specimens. For example, one exploratory excavation about 1m x 1m x 80 cm deep yielded 11 small nymphs. About 50 m distant, an excavation 1 m x 1 m x 30 cm deep yielded five adult males but no nymphs.

The greatest density was recorded at the same site during excavation in late March/early April 2004 when the largest and deepest pit was dug (3 m x 1 m x 1.8 m [in part]). Calculations produced a figure of c. 100 specimens for each square metre of surface. Specimens were absent from the dry A horizon (c. 20 cm deep) but were numerous at all depths of the moist B horizon down to 180 cm. The greatest density occurred in the 60–90 cm deep zone (101 specimens/m^3) and the 160–180 cm deep zone (100 specimens/m^3). The size/frequency distribution of this sample is represented in Figure 28.

At the Horrocks site in August 2003, the author excavated seventeen 1m x 1m pits to a depth of at least 40 cm at various locations around the farm to check for the presence of sandgropers. All were in deep yellow sand under pasture. In one paddock, only C. kochii was found. In an adjoining paddock, mainly Species A was found with an occasional C. kochii. There was very little observable difference between these two paddocks in terms of soil and pasture cover. Several excavations in a paddock situated in a vale produced no specimens at all. Clearly, the distribution of sandgropers is patchy in seemingly suitable habitat, but what factors determine the presence or absence of these insects has yet to be determined.

Food and feeding

Examination of the gut contents of 62 winter-collected and 100 summer-collected specimens of C. kochii and C. tindalei revealed that they had consumed a diversity of materials, most of it being of vascular plant origin although insect and arachnid remains were also identified in many specimens. Fungal tissues, including hyphae, sporangia and spores, were present more often than not, but mostly in small quantities. Sand grains, too, were almost always present throughout the intestine but, comprising only a minor component of gut contents, were probably accidentally ingested with the food. The food was well masticated and finely divided, so identification sometimes required comparison of tissues at the cellular level under a compound microscope.

Sloughed peritrophic membranes were always present in the gut and enclosed the food, regardless of the quantity of the latter.

Ingested plant material consisted mainly of underground parts (roots and stolons) but also comprised aerial parts such as stems and leaves of grasses (including cooch, wheat and barley), dicotyledonous leaves (e.g., Cape Weed), floral bracteoles of Asteraceae, and seeds of several kinds. Most seed tissue was not identified but several specimens of C. kochii from the Horrocks and Dandaragan sites had eaten seeds of 'double-gee' (Emex australis), a pest weed in these areas. Double-gee seeds are contained in hard, spined fruits which the insects evidently chew open.

Plant material varied from fresh (e.g., white rootlet or chlorophyll-containing leaf tissue) to old and partly decomposed (brownish tissue containing lots of fungal hyphae and spores). The presence of chlorophyll-containing leaf tissue matching that of wheat leaves in the intestines of sandgropers collected from wheat fields could be taken as convincing evidence that the insects damage wheat as reported by Richards (1980). There is some possibility, though, that sandgropers may simply be availing themselves of stems and leaves pulled into the soil by cutworms (noctuid moth larvae) rather than being primary pests. On a farm east of Northampton, the author examined a patch of barley crop purportedly thinned by sandgropers. Numerous young barley plants had turned yellow and many loose stems and leaves were found partly pulled into the soil. Excavation around these damaged plants yielded not sandgropers but numerous pink cutworm larvae (Agrotis munda Walker). These cutworms are reported to cause the kind of damage observed (Common 1990).

Fungal tissue in gut samples consisted mostly of rusts, saprophytic and mycorrizal fungi probably ingested with root, stem and leaf tissue. In a few samples, though, significant amounts of fungal tissue suggested direct browsing, one such sample containing VAM (vesicular-arbuscular mycorrhiza) spores (Dr Neale Bougher, pers. comm.).

A variety of invertebrates were identified among gut contents (Table 2). In most cases, the remains of only one or two insects were present. However, two adults of C. tindalei had consumed numerous worker termites, clearly demonstrating purposeful predation rather than accidental ingestion. Most of the listed invertebrates are likely soil inhabitants, even the native bee. Six or more insect egg chorions about 4 mm long and possibly from acridid grasshopper eggs were found in the gut of one adult male of C. kochii.

Cannibalism was encountered in the very dense population of C. kochii at the Dandaragan site among summer-collected specimens (see Table 2). Second and older instar nymphs and adults had consumed first instar nymphs which formed the bulk of the population at the time. In several individuals, the gut contents included fragments of both the front and hind ends of the prey, providing

Table 2   List of arthropod food items identified among the gut contents of *Cylindraustralia kochii* and *C. tindalei* and
the numbers of specimens in which they were found.

Food item	C. kochii	C. tindalei
Dermaptera	1	
Isoptera – workers	2	4
?Orthoptera: ?Acrididae – eggs	1	
Orthoptera: Cylindrachetidae – nymphs	17	
Hemiptera: Fulgoroidea		1
Diptera: Mycetophilidae – larva		1
Diptera: Sciaridae – adult		1
Diptera: Sciaridae – larva	1	
Diptera: Cylcorrapha – larva (1ˢᵗ instar?)		1
Lepidoptera: Noctuidae, *Agrotis* – larva	1	
Lepidoptera: unidentified larva	3	
Coleoptera: Scarabaeidae, Melolonthinae – adult	3	1
Hymenoptera: Formicidae – worker	10	2
Hymenoptera: Colletidae, *Dermatohesma* – adult	1	
Araneae		1
Acarina	2	3
unidentified chitinous remains	7	

convincing evidence of predation as opposed to accidental ingestion.

Evidence that first instar nymphs consume some or all of their eggshells was found in 11 specimens collected at Dandaragan in January and March/April. Among the gut contents were fragments of fenestrated membrane (consistent with the outer layer of sandgroper egg chorion) plus large numbers of colourless, refractive, spherules (diameter *ca.* 0.01 mm). Similar spherules occur in clusters in the inner layer of the egg chorion. Further evidence was obtained when four newly hatched first instar nymphs were maintained in glass vials with their eggshells. Torn edges of the chorions, at first entire, became distinctly serrated

and eroded due to the feeding activity of the nymphs.

When first instar nymphs leave their egg chambers deep in the soil, their most likely food source would be the very fine roots found to lace the soil there.

In terms of gut contents, there were some notable differences between specimens collected in 'winter' (May to September; see Table 3) and those collected in 'summer' (December to April; see Table 4): 93% of winter specimens had eaten plant material compared with only 13% of summer specimens. Only 44% of summer specimens showed evidence of recent feeding and 57% of those had eaten an insect (in 18 of 25 cases, another sandgroper). The

Table 3   Summary of gut contents of sandgroper specimens collected during 'winter' months (i.e. late April to
September) from various localities in south-western Australia.

Species	No. of specimens examined	Numbers of specimens that had eaten certain items		
		Plant material	Seed material	insect/mite
C. kochii	45	42	24	12+
C. tindalei	17	11	3	10

Table 4   Summary of gut contents of specimens of *Cylindraustralia kochii* collected in 'summer' months (i.e., December
to early April) from the Dandaragan site. Cannibalism is represented in the column headed 'Sandgroper'. The
column headed 'Egg chorion' refers to first instars that appear to have consumed their own egg chorion after
hatching. For an explanation of the right-hand column, see under *Predators, Parasites and Associated
Organisms – Amoebae.*

Sample	n	Numbers of specimens that had eaten certain items					
		Any food	Plant matter	Sand groper	Other insects	Egg chorion	Number with amoebae and/or rectal convolutions
Early Dec.	40	6	6	1	2	3?	28
Late January	30	20	5	13	2	2	22
March/April	30	18	2	4	3	9	10
Combined	100	44	13	18	7	14	60

low incidence of plant-feeding during summer might suggest that the insects avoid the dry surface layers of the soil where most of the grass and herb roots occur. In summer, too, cooch grass was the only live plant at the study site. Yet, among the plant material consumed by some summer-collected specimens were grass-leaf and seed tissues. Their presence in specimens collected at depths of 60–95 cm suggests that those individuals had recently ventured to or near the surface to feed.

The occurrence of amoebae in the gut of summer-collected specimens and the seemingly associated condition referred to here as 'rectal convolutions' is discussed in detail below under *Predators, Parasites and Associated Organisms*.

Faecal pellets observed in the rectum, were usually solid, roughly cylindrical, and enclosed in peritrophic membrane.

The gut contents of two adult females of Species B consisted mostly of various plant tissues along with small amounts of arthropod chitin. Günther (1992) and Tindale (1928) recorded plant tissue and insect chitin in the alimentary tracts of a further three species of *Cylindraustralia*, so omnivory is clearly widespread in the genus.

Annual Life Cycle and Development

Adults and nymphs of a broad range of sizes were present in population samples of *C. kochii* collected throughout the year (Figure 28). From the histograms it will be seen that the first and second nymphal instars were by far the most numerous stages present in each sample. The third and fourth instars, by contrast, were very poorly represented, being scarcer even than the fifth instar. As revealed by Table 5, laid eggs were found in the soil at intervals throughout most of the year. The occurrence of eggs and early instars through most months of the year initially suggested the possibility of year-round breeding in *C. kochii*. This possibility, however, is not supported by other observations.

Dissection of adult females collected from May to August revealed that most carried eggs ready to lay in the oviducts or at least had near-mature ova in the ovaries. For example, five adult females

ploughed up on 10 May 2003 all carried eggs ready to lay. By contrast, the ovarioles of the only four females collected in summer (late January and late March) had no ova near egg-size. Instead, each ovariole contained only a series of very small to minute ova. Additionally, the spermathecae of all four females were devoid of sperm. Thus it is likely that these females were very young, pre-reproductive individuals.

At the Dandaragan site, freshly laid (translucent) eggs were found only during the late May and June–July visits. All eggs found later than July through to December were opaque and showed no signs of embryological development. Developed and hatching eggs were only found in January.

Several apparently freshly laid eggs collected in June/July were maintained in the laboratory for several weeks during which time they turned opaque and some succumbed to mould but none hatched. A few were opened to check for signs of embryological development but none was found.

In January 2004, a number of opaque eggs were excavated, some showing signs of development (eye spots and legs vaguely visible through the chorion). On this same occasion, empty egg-shells were found along with tiny, clearly newly emerged nymphs in several chambers. A number of eggs hatched over subsequent days. During a March–April excavation at the same site, only one (opaque) egg was found.

In October 2004, 32 opaque eggs were excavated at Dandaragan and returned to the laboratory. Although a few succumbed to mould attack, turned black and/or shrivelled, most eggs remained outwardly unchanged until late February 2005. Four eggs hatched between 24 February and 1 March 2005 and several more probably would have hatched had they not been dissected to check for embryological development. The first such dissections were on 17 January: two eggs contained small embryos and another a live, almost fully developed larva. On 3 February, a number of eggs were wet with distilled water to varying degrees and over varying periods from one day to two weeks to see if this might induce eclosion. However, these treatments were ineffectual. Eleven

Table 5   Dates when eggs of *Cylindraustralia kochii* were excavated from soil.

Month (days), year	Location	Comments
January (28-31), 2004	Dandaragan	Many, opaque, with embryos or hatching
March (29)-April (1), 2004	Dandaragan	One, opaque
May (28-30), 2003	Dandaragan	Many, translucent
June (30) – July (2), 2003	Dandaragan	Many, translucent
August (20-26), 2003	Horrocks	Two
October (27-29), 2004	Dandaragan	Many, opaque
November (16), 2002	Mullaloo (Perth)	Two, opaque
December (3-6) 2003	Dandaragan	A few, opaque

eggs remaining unhatched on 14 March were dissected and, while life had expired in all of them, embryological development had proceeded to varying stages in several and two contained fully formed larvae.

Four first instar nymphs reared from eggs in late February/early March 2005 were maintained alive in moist soil with germinating mixed budgie seed. They thrived (as evidenced by their increasingly large abdomens) but succumbed to disease one by one, the last surviving for seven months. None moulted to the second instar.

Taking account of the above data, it seems likely that oviposition occurs from May to August; the egg chorion is shiny and translucent at first but gradually turns dull and opaque; eggs remain dormant until mid-summer when they develop and hatch. If it is the norm that hatching is restricted to mid-summer, then the year round presence of first instar nymphs suggests that this stadium endures for at least twelve months. If each instar were to be equally long-lived, the whole life cycle of *C. kochii* would extend over at least five years.

The scarcity of third and fourth instars in most population samples is difficult to explain. Only in the January and March–April 2004 samples were significant numbers of third instar nymphs present (Figure 28). If, as it seems, the life cycle occupies several years, then the absence or scarcity of a particular stage in the population could simply reflect a past year in which fewer eggs were laid or in which mortality of early stages was heavy. In order to gain a clearer and more reliable picture of population structure and change through the year, it will be necessary to gather larger samples. In this study, excavation by spade greatly restricted the area of soil that could be turned over, especially at greater depths. Additionally, it is possible that vibrations caused by digging might have caused some larger specimens to flee the excavation sites via existing galleries. Rearing specimens in captivity will also be necessary to determine longevity in the various instars and reliable data on longevity is necessary to interpret population structure.

Fecundity

Females have ten ovarioles per oviduct. Although a maximum of 14 eggs ready to lay were found in one individual (kept captive in a small container of soil for several weeks and therefore prevented from ovipositing) no more than seven were found in several other adult females. As each egg is laid singly in its own chamber, the rate of egg production must be comparatively low. What is not known is how long females go on ovipositing and how many eggs they would lay in their lifetime.

Mating

No observations of mating were made. Attempts to induce copulation by placing pairs of adults together in small containers proved unsuccessful. However, examination of the copulatory organs of freshly killed adults strongly suggests that mating individuals must come together 'tail' to 'tail' and venter to venter (somewhat as in Figure 20). The phallus cannot be exserted very far and has little flexibility. By making contact as in Figure 20, the hooks on the paraprocts of the male could engage the hind margin of sternite 8 of the female, pulling it down to open the vagina and the phallus would be orientated at just the right angle to permit intromission.

Copulation could hardly occur within the confines of normal galleries but it might occur in the widened sections of galleries noted under *Burrowing* above. Alternatively, copulation might occur on the surface of the ground. To check this possibility, nocturnal searches by torch-light were undertaken where sandgropers were known to be present in dense populations. Searches were made in both wet and dry weather conditions but no surface activity was encountered.

Predators, Parasites and Associated Organisms

According to several farmers, 'crows' (actually ravens) gather in flocks to predate on sandgropers turned out of the soil during ploughing of pastures. Johnstone and Storr (2004) recorded sandgropers from the guts of the Australian Raven. Farmers also report that foxes dig sandgropers from their surface trails and one observer noted the remains of sandgropers in fox scats.

This study found no evidence that sandgropers (either adults or immatures) are subject to attack by insect predators or parasitoids. If truly free of such attacks they would be a rarity among the insects. Evidently, their wholly subterranean existence, perhaps combined with their very hard integuments (anteriorly) and their chemical defences, serve to shield them from such enemies.

Gregarines

The mid guts of many specimens of *C. kochii* and *C. tindalei* were found to contain white bodies up to 2 mm long which superficially resembled insect ova or maggot-like larvae. These proved to be 'gamonts' of protistan parasites of the genus *Gregarina*, class Apicomplexa (formerly Sporozoa). They were present in varying numbers, rarely just one or two, frequently dozens and occasionally hundreds when they packed the lumen of the midgut. Another stage in the life cycle of these organisms, the spherical 'gamontocyst', was observed frequently in faecal pellets in the rectum. Gregarines were found in both adults and nymphs of various sizes from all study sites. Their incidence was comparatively low among dissected specimens collected from May to August, 16 of 50 *C. kochii*

and 3 of 18 *C. tindalei* being infested. Their incidence was very much higher in the early December sample of *C. kochii* from the Dandaragan site, 32 of 38 dissected specimens being infested. However, at the same site, only 3 of 30 dissected specimens from late January and none of 30 from late March/early April were infested. This dramatic reduction could be correlated perhaps with the apparent cessation or significant reduction of feeding observed in summer populations (see under *Food and Feeding*).

Amoebae

Specimens of *C. kochii* collected from the Dandaragan site in summer months exhibited another protistan occupant of the midgut: gold-coloured, single-celled organisms tentatively identified as amoebae. These occurred in varying numbers from just a few up to hundreds in the peritrophic membranes of the mid gut (made more visible by the absence of food material). It appeared that the amoebae did not survive their passage through the gut. Instead, they broke down in the posterior part of the mid gut or in the hind gut where they became concentrated in mucus-like material in narrow peritrophic membrane tubules. In the rectum, the tubules became convoluted and compacted into soft, translucent, honey-coloured pellets. Specimens whose rectal contents consisted only of convoluted tubules almost invariably had amoebae in the mid gut and their intestines were either devoid of food material or contained only minor quantities. Convoluted tubules were noted in 60% of summer-collected specimens (see Table 4 for details). These observations suggest that infestation of the gut by amoebae is associated with (perhaps even causes) a cessation of feeding. Given the absence of feeding, the amoebae are possibly ingested through the imbibition of ground-water (made possible by heavy summer rains). Because the amoebae appear not to survive their passage through the sandgropers, they cannot be considered to be parasites.

Nematodes

Nematodes identified as 'dauers' (non-feeding, resting or dispersal stage larvae) of the family Rhabditidae and possibly the genus *Rhabditis* (Dr Kerrie Davies, pers. comm.) proved to be common occupants of the genital chambers of *C. kochii* and *C. tindalei* in the northern parts of their ranges (north of the latitude of Geraldton). No such genital occupants were found in specimens south of Geraldton. In one specimen of *C. kochii*, dauers occurred also in a depression of the fore femur.

Only about 0.5 mm in length, dauers frequently formed tightly packed masses comprised of dozens or even hundreds of individuals beneath the phallus of male hosts. Dauers were also found in the vaginas of three adult females. When a freshly killed male sandgroper was dissected in saline solution, the nematodes were at first still but, on being disturbed with a needle, quickly became active, flexing their bodies strongly back and forth and dispersed in the saline. In some cases, however, a few to many of the nematodes were dead, brown and stiff.

Only occasional nematodes were encountered among gut contents and were possibly accidentally ingested with the food. None were encountered elsewhere among the internal organs of the insects. At the Dandaragan site, two egg chambers contained dead detached eggs with clusters of nematodes of various sizes on, in and around the latter. These nematodes were identified as bacterial-feeding cephalobids (common soil inhabitants) and an unidentified species, possibly *Mesorhabditis* (Dr Kerrie Davies, pers. comm.). Neither kind represented the same species as the dauers in the sandgropers' genital tracts.

As sandgropers carried dauers only in part of their range and no other part of this particular nematode's life cycle was found to be closely associated with the insects, the nematodes may simply be using them as dispersal agents. Questions remaining unanswered are – how do so many dauers find their way into the genital chambers, where do they come from and are the dauers transferred between the sexes during copulation? Sexual transmission of nematodes has been reported to occur in certain other orthopterans (e.g., Luong *et al.* 2000).

Mites

Phoretic deutonymphs (non-feeding, dispersal stage nymphs, also known as hypopi) of six species of mites were found externally on a number of individuals of *C. kochii* and *C. tindalei*. They occurred, sometimes singly, sometimes clustered, on various sheltered parts of the body: inner sides of fore legs, flanks of abdomen beneath mid and hind femora, and in folds of abdominal segments. These mites were identified by Dr Barry O'Connor (pers. comm.) and their names and host associations are listed in Table 6. Dr O'Connor noted that some members of unnamed genus 1 are associated with termites in the USA and central America while unnamed genus 2 is similar to taxa (e.g., *Forcellinia*) associated with ants and termites.

Fungi

Many dead eggs were found in chambers during excavation at the Dandaragan site in July and most of these were heavily coated with various kinds of fungi. Even seemingly fresh, suspended eggs often had fungal hyphae (bright yellow, black or colourless) growing over their surfaces and some were dotted with fungal sporangia.

Table 6   Mites recorded from the bodies of sandgropers in the present study.

Mite taxa	C. kochii	C. tindalei
Order Acariformes: Suborder Astigmata		
Acaridae – unnamed genus 1	+	
Acaridae – unnamed genus 2, species 1		+
Acaridae – unnamed genus 2, species 2	+	
Acaridae – *Sancassania* sp.	+	
Histiostomatidae, *Histiosoma* sp.		+
Order Parasitiformes: Suborder Mesostigmata		
Ascidae? (*Lasioseius*?)	+	

Defences

No biting or other defensive behaviours were observed while handling specimens except that, when restrained, the insects sought to 'burrow' their way to freedom with their powerful fore legs. When exposed during excavation, the insects always attempted to burrow back into the soil or withdrew into their galleries.

The characteristic odour produced by sandgropers (see above under *Odour glands*) probably serves a defensive function.

CONCLUSION

Many Tridactyloidea are heavily dependent on fresh-water bodies for their survival. Some 'pygmy mole crickets and mud crickets' (Tridactylidae and Ripipterygidae, resp.) inhabit the margins of lakes, streams and rivers, often in humid tropical environments, where they burrow and feed in the damp surface layers of mud or sand (Günther 1994). The Argentinian cylindrachetid, *Cylindroryctes spegazzinii* (Giglio-Tos), lives in the gritty shores of lakes and associated rivers (Günther 1992). *Cylindraustralia* species, however, live well away from free water and many inhabit semiarid to arid habitats. Nevertheless, the present study has indicated that they are still dependent on soil moisture and no specimens were ever found in truly dry soil.

Despite the gains from the present study, many basic questions concerning cylindrachetid biology remain to be answered, even for the principal subject *C. kochii*. For example, how long is the complete life cycle? How long do adults survive? Where, when and how do they mate? How many eggs does a female produce in her lifetime? Are there any insect predators or parasitoids not found in this study? At what rates do sandgropers burrow near the surface and at depth? Do they continually burrow into fresh soil or do they (at least at times) return to home burrows? Do they exhibit daily patterns of activity?

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REFERENCES

Barrett, C. (1928). Notes on *Cylindracheta*. *Victorian Naturalist* **44**: 266–267.

Common, I.F.B. (1990). *Moths of Australia*, Melbourne University Press, Carlton, Victoria.

CSIRO (1991). *The Insects of Australia. A textbook for students and research workers* (Second edition), Melbourne University Press, Carlton, Victoria.

Flook, P.K., Klee, S. and Rowell, C.H.F. (1999). Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. *Systematic Biology* **48**: 233–53.

Gambardella, L.A. de (1971). Oviposicion y eclosion de *Rhipipteryx notata* Burm. 1838. *Revista Peruana de Entomologia* **14**: 282–285 (cited by Günther (1994); not seen).

Günther, K.K. (1992). Revision der Familie

Cylindrachetidae Giglio-Tos, 1914 (Orthoptera, Tridactyloidea). *Deutsche Entomologische Zeitschrift* **39** (4/5): 233–291.

Günther, K.K. (1994). Die Tridactyloidea-Fauna Kolumbiens (Orthoptera, Caelifera). *Deutsche Entomologische Zeitschrift* **41**(1): 45–56.

Johnstone, R.E. and Storr, G.M. (2004). *Handbook of Western Australian birds. Volume II. Passerines (blue-winged pitta to goldfinch).* Western Australian Museum, Perth.

Kevan, D.K.M. (1989). Grigs that dig and grasshoppers that grovel. *Revue d'Ecologie et de Biologie du Sol* **26**: 267–289.

Lawrence, J.F. and Britton, E.B. (1994). *Australian Beetles,* Melbourne University Press, Carlton, Victoria.

Luong, L.T., Platzer, E.G., Zuk, M. and Giblin-Davis, R.M. (2000). Venereal worms: sexually transmitted nematodes in the decorated cricket. *Journal of Parasitology* **86**: 471–477.

Rentz, D.C.F. (1996). *Grasshopper Country: the abundant orthopteroid insects of Australia.* University of New South Wales Press, Sydney.

Richards, K.T. (1980). The sandgroper – a sometimes not-so-friendly Western Australian. *Journal of Agriculture – Western Australia* **21**: 52–53.

Schremmer, F. (1972). Ein Massenvorkommen von bodenbewohnenden *Rhipipteryx forceps* (Tridactyloidea) in den kolumbianischen Anden. *Pedobiologia* **12**: 317–322 (cited by Günther (1994); not seen).

Tindale, N.B. (1928). Australian mole crickets of the family Gryllotalpidae (Orthoptera). *Records of the South Australian Museum* **4**: 1–42.

Urquhart, F.A. (1973). Some notes on the sand cricket (*Tridactylus apicalis* Say). *Canadian Field-Naturalist* **51**: 28–29 (cited by Günther (1994); not seen).

Uvarov, B. (1966). *Grasshoppers and Locusts, a Handbook of General Acridology,* vol. 1, Cambridge University Press, Cambridge

Wiley, T. (2000). Insect pests of the perennial fodder shrub tagasaste. Farmnote 48/2000, Western Australian Department of Agriculture, Perth.

Zuk, M. (1987). The effects of gregarine parasites on longevity, weight loss, fecundity and developmental time in the field crickets *Gryllus veletis* and *G. pennsylvanicus. Ecological Entomology* **12**: 349–354.